BREVIORA

Museum of Comparative Zoology

CAMBRIDGE, MASS. MAY 29, 1962 NUMBER 158

A FOSSIL GERRHOSAUR FROM THE MIOCENE OF KENYA (REPTILIA: CORDYLIDAE)

BY RICHARD ESTES[1]

Many thousands of fossils, both plant and animal, have been collected since 1947 in the Kavirondo Gulf area, Lake Victoria, Kenya. Most of these fossils come from sediments on Rusinga and Mfanganu Islands, within the Gulf. The vertebrate fauna is diverse, though principally mammalian; thus the discovery of the fossil lizard described here is of special interest. Much of the fossil mammalian fauna has been described in a British Museum of Natural History series (see e.g. LeGros Clark and Leakey, 1951; Whitworth, 1958). Part of the extensive seed-nut flora has recently been described by Chesters (1957). Leakey (1952) has noted and figured some of the remarkably well-preserved invertebrates.

The age of the fossils in this sequence has been assigned entirely on faunal grounds, and is usually considered to be early Miocene (Burdigalian). The reasons for this age determination are given in the papers mentioned above. The presence of both archaic and modern elements in the mammalian fauna as well as our lack of knowledge of the Cenozoic sequence in tropical areas make it difficult to assign a firm date to these deposits. Suggestions ranging from Oligocene to "considerably younger than the lower Miocene" (LeGros Clark and Leakey, 1951) have prompted Whitworth (1958, p. 45) to state that "it is clear that the question of geological age may have to be revised when the description of the East African fossils is completed."

[1] Department of Biology, Boston University, and Research Associate, Museum of Comparative Zoology, Harvard University.

Class Reptilia

Order Sauria

Family CORDYLIDAE

Subfamily GERRHOSAURINAE

Gerrhosaurus cf. G. major Duméril

Referred specimen. — Coryndon Museum, Nairobi, M. F. W. 1955/1.

Locality. — Mfangano Island, Lake Victoria, Kenya, Africa. Area B, of Red Earth Series as mapped by Whitworth (1953). An extensive flora and invertebrate fauna have also been collected from these deposits, but have not yet been described.

Age. — Early Miocene (Burdigalian?).

Preservation and major features of the specimen. — As preserved, the total length of the specimen is 55 millimeters. It consists of most of the head and the greater part of the neck, though it is probable that much more if not all of the entire body was originally present. The external features, many of them from the soft anatomy, are in part completely replaced with calcite. Some bone is preserved internally, but selective replacement has occurred. The external calcite covering is about 3 or 4 millimeters thick, and internal to this the neck and posterior skull region are filled with a soft waxy black sediment which contains small calcite crystals. No trace of the posterior bones of the skull is visible. The head is slightly twisted to the left, and the half-open mouth is filled with calcite. A striking feature of this specimen is the replacement of the tongue by calcite, though no important details of structure are visible. Dorsally, especially in the neck and posterior skull region, the specimen is heavily crushed; otherwise, there is little distortion. The shape of the depression in the top of the skull, the half-open mouth, and lack of crushing in the facial segment suggest that the animal may have been stepped on, perhaps by the sharp hoof of a grazing animal. This might have caused the animal's death, or could also have happened shortly after it was buried by sediment.

The palatal, facial, and marginal bones of the snout are broken or missing. Most of the teeth are eroded, though their outlines are preserved as imprints in the calcite filling of the mouth, but in some places a few tooth crowns still remain, as well as fragments of tooth shafts.

The eye sockets are completely filled with calcite, though the right one is badly eroded. On the left side, the calcite has taken an impression of the underside of the supraorbital plates, but their number cannot be determined. One of the most unusual features of this specimen is the preservation of the external shape of the left eye, in calcite. The lids are sharply delineated, and between them, a low, domed area reflects the outline of the cornea or perhaps the underlying lens.

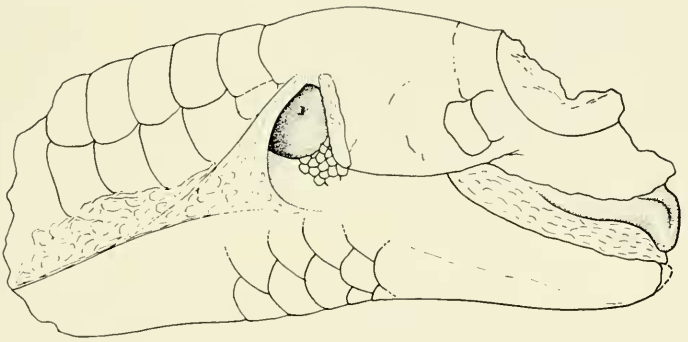

Fig. 1. *Gerrhosaurus* cf. *G. major*, Lower Miocene, Kenya, right lateral view, x 1.5.

The outline of the outer ear and tympanum is perfectly preserved on the right side, though on the left much of it is broken away. The anteroposterior diameter of the ear opening is less on the left as a result of twisting of the head. Many of the granular scales which surround the ear region and extend into the lateral fold are clearly visible. The tip of the extracolumella is strongly imprinted on the tympanum. The lateral fold is prominent on both sides, but is especially clear on the right, where it has been stretched open by twisting of the body on the median axis before deposition.

Very little remains of the posterior skull bones. A thin film of prefrontal and palatine surrounds the left eye, and directly below, small portions of the vomers protrude. Maxillae and dentaries are badly broken, and little remains other than thin edges of their internal processes. Under both eyes parts of the internal faces of the jugals are visible as imprints.

Dorsally, there are imprints of seven or eight postcranial scale rows. They end anteriorly near a smooth flat surface which

represents the skull roof, but whatever bone or scale imprints may have been preserved are no longer present.

Description. — The large imbricate osteoscutes of the throat region are compound; each is formed of multiple polygonal or trapezoidal osteoderms. The anterior ones are small, smooth, and subequal, the posterior ones elongated and either smooth or faintly wrinkled. The posterior borders of the osteoscutes are rounded or slightly squared. The throat osteoscutes are in seven longitudinal rows between the lateral folds, and they alternate rather than being aligned in straight transverse rows. Posteriorly, their arrangement is somewhat distorted as a result of post-mortem dislocation of some of the scales. Two pairs of large non-imbricate chin shields seem to have been present, formed of small subequal polygonal osteoderms.

The lateral folds appear to have contained small or granular scales, but this is uncertain. Both folds extend as far forward as the ear.

The subtriangular outer ear opening is covered ventrally with small squarish or lenticular scales which grade into those of the lateral fold. On the posterior border of the ear opening, several marginal rows of small scales are followed by a row of slightly larger ones. The tympanic shield is strap-shaped, narrow, and not at all posteriorly expanded.

The dorsal scales of the neck, of which imprints of seven or eight straight transverse rows are preserved behind the occipital margin, are large and subrectangular.

Abrasion has removed almost all imprints of scales from the cheek, but a few large ones are visible anteriorly.

The pleurodont teeth are robust, tall, and columnar. Imprints of their closely-spaced shafts indicate that replacement teeth were formed in subcircular basal excavations. Preserved tooth crowns are faintly tricuspid.

Discussion. — Union of the gerrhosaurs and cordylines as subfamilies of the Cordylidae, as recently suggested by McDowell and Bogert (1954), is undoubtedly correct. The presence of compound osteoderms in cordylines (*sensu stricto*), a character not mentioned by these authors, further emphasizes the separation of this group from the anguimorphs and allies them with the scincomorphs.

Until now, the cordylids have had no clear fossil record. *Pseudolacerta mucronata* (Filhol) has been tentatively placed in this family by Romer (1956, p. 552). De Stefano (1903, p. 413)

and Filhol (1877, p. 489) do not mention any characters of taxonomic value, and Filhol's illustration (*ibid.*, fig. 423) is vague and diagrammatic. Hoffstetter (1944, p. 553) considers it possibly a skink, but notes that vertebrae similar to those of *Cordylus* (*sensu latu*) occur in the same deposit. Later, he indicates (1955, p. 621) that these fossils "rappellent les pièces homologiques de l'actuel *Cordylus*," but the assignment is still tentative.

The fossil described here is referable to the subfamily Gerrhosaurinae on the basis of the large, broadly imbricate, rounded or slightly squared throat scales, contrasting with the much smaller, non-imbricate, diamond-shaped throat scales of the cordylines. *Chamaesaura* has larger throat scales than other cordylines, but they are anteroposteriorly elongate and mucronate, rather than smooth and transversely widened as in gerrhosaurines.

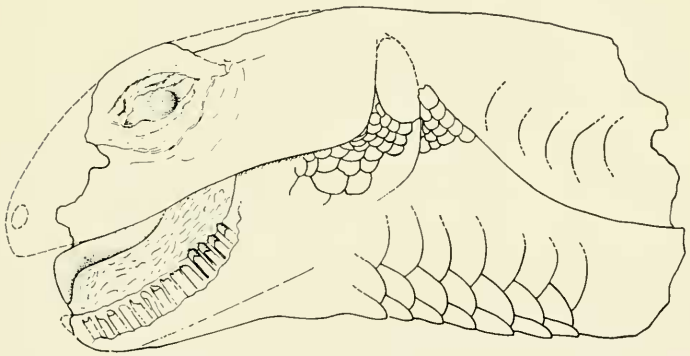

Fig. 2. *Gerrhosaurus* cf. *G. major*, Lower Miocene, Kenya, left lateral view, x 1.5.

Though the published generic characters of *Gerrhosaurus* are in soft anatomy and scale details not preserved here (Loveridge, 1942, p. 488; FitzSimons, 1943, p. 268), similarity between this fossil and Recent members of the genus seems to indicate that it belongs here. The throat scales, what remains of the dorsal scales, shape of the ear and lateral fold all agree closely with these characters of the Recent genus. Moreover, a number of resemblances discussed below strongly suggest reference to the Recent species *G. major*.

1. The fossil has the size and general proportions of a large adult individual of *G. major*. The latter is the largest of the species of *Gerrhosaurus;* most other species are considerably smaller.

2. The shape of the opening of the external ear in *G. major* may be rounded or slightly angular dorsally. In the available specimens, *G. m. major* most frequently shows the rounded condition, but *G. m. grandis* usually has a more angular dorsal edge, as in the fossil. *G. m. bottegoi* resembles *G. m. major* in this character.

3. In gerrhosaurs, the shape of the tympanic shield is considered taxonomically significant. This scale lies on the anterior border of the outer ear, and in all species of *Gerrhosaurus* except *G. major*, is thin, flattened, and often expanded to cover and protect the cavity of the outer ear (see e.g. FitzSimons, 1943, figs. 150, 156). Loveridge (1942, pp. 515, 518) states that tympanic shields of *G. flavigularis* are also narrow and band-like as in *G. major*. This is grossly true, but in detail the two can be distinguished easily. *G. flavigularis* has a narrowly crescent-shaped tympanic shield (see e.g. FitzSimons, *ibid.*, fig. 154; cf. fig. 164 of *G. m. grandis*) which is thin and flattened, while that of *G. major* is strap-shaped, and thickened.

4. Another similarity to *G. m. grandis* is the presence, on the posterior border of the outer ear opening, of a small anterior row of scales, flanked by a larger posterior row. In *G. m. major* and *G. m. bottegoi* these scales tend to be subequal. This character varies somewhat, and in any case the time separation as well as lack of further preserved characters precludes reference of this fossil to one of the living subspecies. However, this character and that given as number 2 above seem to suggest a closer relationship to *G. m. grandis* and *G. m. bottegoi* than to *G. m. major*. The other subspecies, *G. m. zechi*, is known from only a few specimens, none of which were available to me. It is very closely related to *G. m. bottegoi* and its status is not clear at this time.

Distribution of Recent *Gerrhosaurus major*

G. major occurs today in principally arid savanna along the eastern coast of Africa, north to Eritrea and south to Zululand. *G. m. grandis*, the most southern subspecies, is found from Zululand north to Morogoro, Tanganyika. *G. m. major* is a coastal

subspecies, principally in Tanganyika, but reaching as far north as Kenya. *G. m. bottegoi* ranges from central Tanganyika north through central Kenya and reaches north to coastal Eritrea, farther north than any other gerrhosaur, and is the only subspecies of *G. major* found today in the Kavirondo Gulf region of Lake Victoria, the same region as the occurrence of the fossil. The problematical *G. m. zechi* has, so far as known, a disjunct distribution limited to the northern Belgian Congo and Togo.

CONCLUSIONS

The fossil described here is closely related to, and perhaps conspecific with, the Recent species *Gerrhosaurus major*. Thus it is extremely probable that the habitat of the lizards represented by the fossil was semi-arid or arid savanna, like that of the modern species. The presence of a mammalian fauna of

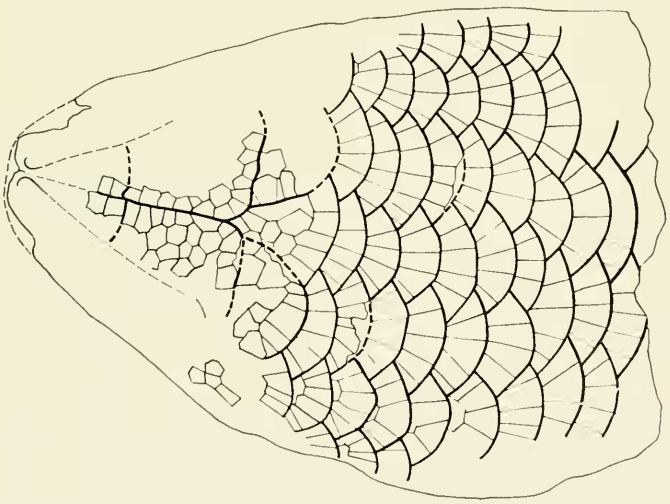

Fig. 3. *Gerrhosaurus* cf. *G. major*, Lower Miocene, Kenya, ventral view, x 1.5.

dominantly savanna aspect in these deposits supports this conclusion. Whitworth (1953, p. 82) states that ephemeral lakes were probably present in this region in the late Miocene, allowing the savanna mammals access during the periods of desiccation indicated by the sediments. He also points out that similar

situations occur today in areas of the northwestern Sudan. Chesters (1957), on the basis of the flora, has concluded that a "gallery-type forest in which trees festooned with climbers overhung the watercourses" lived near to the site of deposition, and that many of the fossil nuts and seeds represent living tropical African genera.

Close relationship of the fossil with the Recent species indicates that at least part of the pattern of speciation seen within the genus today is of considerable antiquity. Moreover, similarities of the fossil to some of the Recent subspecies of *G. major* perhaps indicate that some of the geographic variants seen today were beginning to appear, as far back as the Miocene. The two Recent subspecies which the fossil most closely resembles, *G. m. bottegoi* and *G. m. grandis*, are northern and southern populations which intergrade in the area immediately south and east of Lake Victoria. It is interesting, but highly speculative, to suggest that the occurrence of the fossil near the present area of intergradation of these two Recent subspecies might either indicate a stage in the development of the Recent subspecific patterns, or an intergrade between the two which could possibly be duplicated today if sufficient specimens were available.

Moreau (1951, esp. pp. 877, 881) has gathered evidence which suggests that at least from the mid-Cenozoic to the present, central and eastern Africa had a climate and broadly defined vegetational types which differed relatively little from those occurring there today. If this is so, the above alternatives are quite possible, yet additional fossil evidence, both biotic and climatic, is necessary to accept or reject either of them.

SUMMARY

The well-preserved head of a fossil lizard from the Lower Miocene (Burdigalian?) of Mfanganu Island, Lake Victoria, Kenya, is tentatively referred to the Recent species *Gerrhosaurus major* (Reptilia: Cordylidae). Many external features of soft anatomy are preserved as casts in calcite, including the eye, tongue, and tympanic membrane. Close relationship to the Recent semi-arid or arid savanna species indicates a similar habitat for the fossil, a conclusion corroborated by the savanna aspect of the fossil mammals from contemporaneous deposits on nearby Rusinga Island. This specimen is one of the oldest vertebrate fossils even tentatively referred to a Recent species and must indicate that at least part of the pattern of speciation seen in Recent gerrhosaurs is of relatively ancient origin.

LITERATURE CITED

Chesters, K. I. M.

1957. The Miocene flora of Rusinga Island, Lake Victoria, Kenya. Palaeontogr., Abt. B, **101**:30-71, 4 figs., 21 pls.

De Stefano, G.

1903. I sauri del Querey appartenenti alla collezione Rossignol. Atti Soc. Ital. Sci. Nat., **42**:382-418, 2 pls.

Filhol, H.

1877. Recherches sur les phosphorites du Querey. Étude des fossiles qu'on y rencontre et spécialement des mammifères. Ann. Sci. Géol., **8**:1-561, 55 pls.

FitzSimons, V. F.

1943. The lizards of South Africa. Transvaal Mus., Mem. no. 1, xv + 528 pp., 384 figs., 24 pls.

Hoffstetter, R.

1944. Sur les Scincidae fossiles. I. Formes européennes et nord-américaines. Bull. Mus. Nat. Hist. Nat. Paris, **16**:547-553, 2 figs.

1955. Squamates du type moderne. *In:* Piveteau, Traité de Paléontologie, 5:606-662, 26 figs.

Leakey, L. S. B.

1952. Lower Miocene invertebrates from Kenya. Nature, **169**:624-625, 2 figs.

LeGros Clark, W. E., and Leakey, L. S. B.

1951. The Miocene Hominoidea of East Africa. Brit. Mus. Nat. Hist., Fossil Mammals of Africa, no. **1**:1-117, 28 figs., 9 pls.

Loveridge, A.

1942. Revision of the African lizards of the family Gerrhosauridae. Bull. Mus. Comp. Zool., Harvard Univ., **89**:484-543.

McDowell, S. B., Jr., and Bogert, C. M.

1954. The systematic position of *Lanthanotus* and the affinities of the anguinomorphan lizards. Bull. Amer. Mus. Nat. Hist., **105**:1-142, 43 figs., 16 pls.

Moreau, R. E.

1951. Africa since the Mesozoic, with particular reference to certain biological problems. Proc. Zool. Soc. London: **121**:869-913, 4 tables.

Romer, A. S.

1956. Osteology of the Reptiles. Univ. Chicago Press, xxi + 772 pp., 248 figs.

Whitworth, T.

1953. A contribution to the geology of Rusinga Island, Kenya. Quart. Jour. Geol. Soc. London, **109**:75-96, 2 pls.

1958. Miocene ruminants of East Africa. Brit. Mus. Nat. Hist., Fossil Mammals of Africa, no. **15**:1-50, 18 figs., 12 tables.

Plate 1

Gerrhosaurus cf. *G. major*. Photograph of left lateral view. Skull crushed dorsally. Note especially outline of eyelids and cornea, slightly protruding tongue, and well-preserved scale outlines. Not to scale. Slightly retouched. Photograph by Frederick Maynard, Boston University.